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The hyporheic habitat of river ecosystems

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Contemporary river ecology is based primarily on biogeochemical studies of the river channel and interactions with shoreline vegetation, even though most rivers have extensive floodplain aquifers that are hydraulically connected to the channel. The hyporheic zone, the interstitial habitat penetrated by riverine animals, is characterized as being spatially limited to no more than a few metres, in most cases centimetres, away from the river channel[1-9]. However, riverine invertebrates were collected in hundreds per sample within a grid of shallow (10 m) wells located on the floodplain up to 2 km from the channel of the Flathead River, Montana, USA. Preliminary mass transport calculations indicate that nutrients discharged from the hyporheic zone may be crucial to biotic productivity in the river channel. The strength and spatial magnitude of these interactions demonstrate an unexplored dimension in the ecology of gravel-bed rivers.

The Flathead River, a major tributary of the Clark Fork of the Columbia, drains a catchment area of 22,241 km^2 (average flow $= 340\ m^3\ s^{-1}$) in northwestern Montana and southeastern British Columbia. The morphology and surficial geology of the Kalispell Valley (Fig. 1) were largely determined by Pleistocene glaciation. Fine-grained lacustrine sediments and fault traces delineate the northern geological boundary of the palaeodeltas of proglacial Flathead Lake. The river is heavily braided in the area delineating this boundary or ectone (E in Fig. 1). An alluvium of cobbles, gravel and sand covers an impermeable clay formation of Tertiary age upstream of the heavily-braided reach.

Groundwaters in this alluvium interact hydraulically with the Flathead River and a tributary system, the Whitefish River (Fig. 1). Wells near the river channel produced hydrographs that closely tracked daily and seasonal changes in river flow (Fig. 2). Even wells in the centre of the valley, 2 km or more from the rivers, were influenced by river-flow patterns (Fig. 2). The aquifer lies on a 2° slope, bounded on both sides by the river channels; water flows through the system in a north to south direction at an average rate of $0.7\ m^3\ s^{-1}$. The primary area of aquifer discharge is near the confluence of the two rivers, where faulting and finer sediments on the proglacial Flathead Lake palaeodeltas begin to limit groundwater flow rates (E in Fig. 1). Water also moves to and from the channels. During spring freshet, water moves into the aquifer from the river channel until a hydrological equilibrium occurs or river flow begins to decrease. As flows decrease, aquifer water is discharged from the hyporheic zone into the river.

Spatial plots of specific conductance data (Fig. 1) also demonstrated lateral dilution. The 35 mS per metre isopleth (Fig. 1) appeared to delineate true interstitial groundwaters that are inhabited by subterranean fauna[10-14] and are less interactive with surface waters.

This was confirmed by the distribution and abundance patterns of the interstitial fauna within the aquifer. Biota collected from wells in the hyporheic zone (as defined by the 35 mS per metre isopleth, Fig. 1), consisted almost exclusively of stonefly (Plecoptera) larvae and other typically riverine taxa (Table 1). In contrast, subterranean forms were abundant in most of the wells located on the high concentration side of the 35 mS per metre isopleth. There was some overlap between riverine and subterreanean taxa in several wells located near the 35 isopleth, but either subterranean amphipods (*Stygobromus* spp.) or stonefly larvae were very abundant (hundreds per sample), never both.

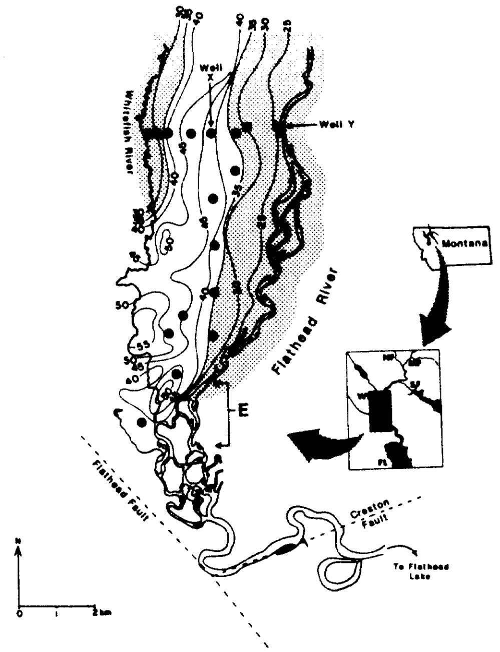

Fig. 1 Map of hyporheic habitat (stippled areas) within the Kalispell Valley of the Flathead River. Isopleths of specific conductance (mS per metre) were determined from 271 wells. Closed circles locate only those wells from which biological samples were obtained. Inset map shows the three major tributaries upstream of the study site. NF, North Fork; MF, Middle Fork; SF, South Fork; the Whitefish River (WF) and Flathead Lake (FL). The area designated E is the interface between porous and less transmissive substrata (see text).

Levels of dissolved oxygen within the wells were always greater than 50% saturation. Temperatures remained at 7-9 °C throughout the year in all wells, except those located near the river channel where greater exchange of water elevated or reduced temperatures in a seasonal way. It may be that the biota navigate through the interstitial groundwaters by following thermal cues when near the river channel, or ion concentration gradients when far from the river.

Table 1 Relative abundance of biota

Hyporheic zone	
Paraperla frontalis (Insecta: Plecoptera)	100
Isocapnia 4 spp. (Insecta: Plecoptera)	100
Chironomidae (Insecta: Diptera)	10
Capniidae (Insecta: Plecoptera)	20
Early instar zoobenthos	20
Incidental zoobenthos	20
Phreatic zone*	
Stygobromus 2 spp. (Crustacea: Amphipoda)	100
Cyclopoid copepods (Crustacea: Eucopepoda)	100
Asellus sp. (Crustacea: Isopoda)	10
Bathynellidae (Crustacea: Bathynellacea)	10

Biota were collected from 17 wells located within the alluvial aquifer adjacent to the Flathead River and on either side of the 35 mS per metre specific conductance isopleth, which differentiated phreatic (>35 mS per metre) and hyporheic (<35 mS per metre) habitats. Data are the percentage of total wells located in either the phreatic or hyporheic zones in which a particular taxon was present in numbers greater than 10 per well on every sampling date ($n = 8$) in 1984-6.

* All taxa listed under phreatic zone are crustaceans of subterranean facies. Bathynellids and *Stygobromus* are exclusively subterranean groups. *Asellus* (*Caecidotea*) sp. is a blind, depigmented isopod of attenuated morphology. Although most cyclopoid copepods are planktonic or littoral, several species are widespread in interstitial biotopes[10-14].

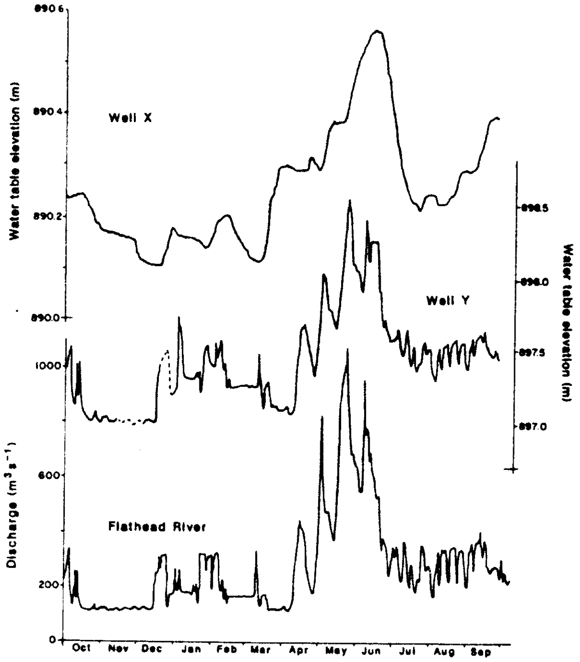

Fig. 2 Hydrographs from wells X and Y (see Fig. 1) compared with the Flathead River in 1984–85. Nonseasonal fluctuations were caused by discharges from a large hydroelectric dam on an upstream tributary (SF in Fig. 1). Well X is 2.4 km and Well Y 50 m from the Flathead River channel.

On the basis of the relative distribution of the biota and the 35 mS per metre isopleth, we were able to measure the hyporheic habitat within the 10 km (approximately) study area (Fig. 1). The hyporheic zone is on average about 3 km wide with an average depth of about 10 m; whereas, the Flathead River channel (median flow) is about 50 m wide with most zoobenthos in the upper 0.25 m of channel substrata. There is therefore about 0.3 km^3 of hyporheic habitat, compared to about 125,000 m^3 of channel habitat. Standing crop biomass in the hyporheic zone could easily exceed benthic biomass in this river.

Stoneflies are apparently the top consumers within an as yet undescribed and probably detritus-based food chain. Others[4,15] have suggested that the hyporheic zone is a functional sink for fine (<500 μm) particulate organic detritus from the channel. Particulates may also be recruited by infiltration of precipitation through the soil profile. Decomposition of organic detritus, coupled with ionic leaching, desorption and other biophysical processes, like nitrification, may sequester labile (bioavailable[16]) nutrients within groundwaters. Nutrient concentrations were significantly higher in the hyporheic (for example well X, Table 2) than in the river. Preliminary calculations of mass transport

Table 2 Average concentrations and standard deviations of nutrients at well sites

Sampling site	Soluble reactive phosphorus	Soluble total phosphorus	Nitrite + nitrate nitrogen	Soluble organic carbon
Well X	1.5 ± 0.5	4.9 ± 1.0	916.0 ± 11.0	$1{,}810 \pm 138$
Well Y	1.2 ± 0.5	2.2 ± 0.8	145.0 ± 5.0	$1{,}810 \pm 112$
River	BDL*	2.3 ± 0.4	38.0 ± 1.0	$1{,}730 \pm 162$

Concentrations are in μg per litre. Well sites were located 2.5 km (well X) and 50 m (well Y) from the Flathead River channel compared to values in the river. These data summarize six bimonthly sampling dates during 1984–85.

* Below detection limit = 1.0 $\mu g\, l^{-1}$.

of bioavailable phosphorus[16] and nitrate-nitrogen indicate that baseflow loads in the Flathead River increased by 25% and 12% respectively. During extended baseflow periods, certain near-shore areas of the relatively unproductive Flathead River channel are matted with algae. We believe that these areas of enhanced phytobenthos production occur in direct response to the inflow of nutrient-rich hyporheic waters.

Gravel-bed rivers are common worldwide[17]. The practice of screening groundwater monitoring wells accounts for the absence of faunal records in samples collected by hydrogeologists. The spatial extent and strength of hyporheic-channel interactions undoubtedly vary from river to river. Nonetheless, hyporheic-channel interactions as reported here are probably common features of gravel-bed river segments, and should be included in holistic constructs[18] of riverine ecosystems.

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